



A new South American Miocene species of 'one-holed' sand dollar (Echinoidea: Clypeasteroida: Monophorasteridae)

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Abstract

A new species of monophorasterid sand dollar, *Monophoraster telfordi* n. sp., is described from the Early Miocene basal horizons of the Chenque Formation of Patagonia, Santa Cruz Province, in southern Argentina. The new taxon raises the number of known species in the family to six, and represents first unequivocal record of the genus for the Early Miocene of South America. It is therefore also the oldest member of the genus. *M. telfordi* is characterized by its test width to length ratio, which is much higher than for the other two described species in the genus, but less than that known for the extremely wide members of the sister taxon, *Amplaster*. *M. telfordi* is also unusual among monophorasterids in lacking broad continuity between basicoronal and post-basicoronal plates in the oral interambulacra. A key is provided to all the known species of Monophorasteridae.

Key words: Clypeasteroida, Monophorasteridae, sand dollars, new taxon, Argentina, Patagonia, early Miocene

Introduction

Recent discoveries suggest that the fossil clypeasteroid fauna (sand dollars and allied forms) of South America is much richer than once thought. At the time of Durham's (1955; 1966) monographs of the clypeasteroids, only a handful of species were known from South America. Prior to the 1960s, it was generally accepted that if the test was characterized by a single perforation, or lunule, located just anterior to the anal opening in the posterior interambulacrum, then it belonged to a species of *Monophoraster*, but if this lunule was lacking, then the specimen belonged to *Iheringiella patagonensis* (Desor, 1847). Since the middle of the last century, South American representatives of the genera *Eoscutella* Grant and Hertlein, 1938, *Abertella* Durham, 1953, and *Amplaster* Martínez, 1984 have been described (Martínez 1984; Parma 1985; Rossi de García & Levy 1986; Mooi *et al.* 2000; Martínez *et al.* 2005; Kroh *et al.* 2013). With this new richness of taxa and biogeographic data, past speculations concerning the origins and subsequent diversification of the South American clypeasteroid fauna (for example, Seilacher 1979) will need to be revisited and new taxa, such as the one described herein, will have to be integrated with such scenarios.

Monophorasterids comprise a small but important clade of New World sand dollars that are found most commonly in the Patagonian region. As revised by Mooi *et al.* (2000), there are two genera, *Monophoraster* Lambert and Thiéry, 1921 and *Amplaster* Martínez, 1984. There is some dispute concerning the stratigraphic range of the monophorasterids, as the type species of *Monophoraster*, *M. darwini*, has been reported to occur in the Eocene of Chile, and there is uncertainty in stratigraphic constraint for many of the rocks in which monophorasterid fossils occur. However, the vast majority of the records for *Monophoraster* and *Amplaster* can be attributed to the Miocene (Mooi *et al.* 2000), as can the strata containing the new species described herein.

Monophorasterids are significant in being characterized by a single lunule in the posterior interambulacrum. This lunule passes completely through the test from the oral to the aboral surface just anterior to the periproct (anal opening). Strong similarities among, and phylogenetic distribution of this so-called anal lunule throughout the mellitid + monophorasterid clade (see Mooi *et al.* 2000) strongly suggest that it is homologous among mellitids, *Monophoraster* and *Amplaster*. The origin of the anal lunule is a unique evolutionary event (Telford 1988). Therefore, the anal lunule is not homologous with the ambulacral lunules found among the mellitids, scutasterids, and astriclypeids. However, the anal lunule does appear to represent a synapomorphy of the mellitid + monophorasterid clade (Mooi *et al.* 2000). Therefore, any new taxa and stratigraphic data for monophorasterids will offer crucial information towards our understanding of the evolution of lunulate, scutelline clypeasteroids.

With its strongly alate shape, the new species of *Monophoraster* described herein is superficially similar to some representatives of the monophorasterid genus *Amplaster*. It is, however, clearly differentiated from the latter by the extreme "pinching" or attenuation of the interambulacra at the ambitus, a slightly smaller anal lunule, placement of the periproct further from the lunule, and narrower contact between the basicoronal and paired post-basicoronals of the posterior interambulacrum. With new information concerning these and other features offered by the new species, evolutionary events among *Monophoraster* and *Amplaster* species can be further explored, and variation among the features better assessed for the Monophorasteridae.

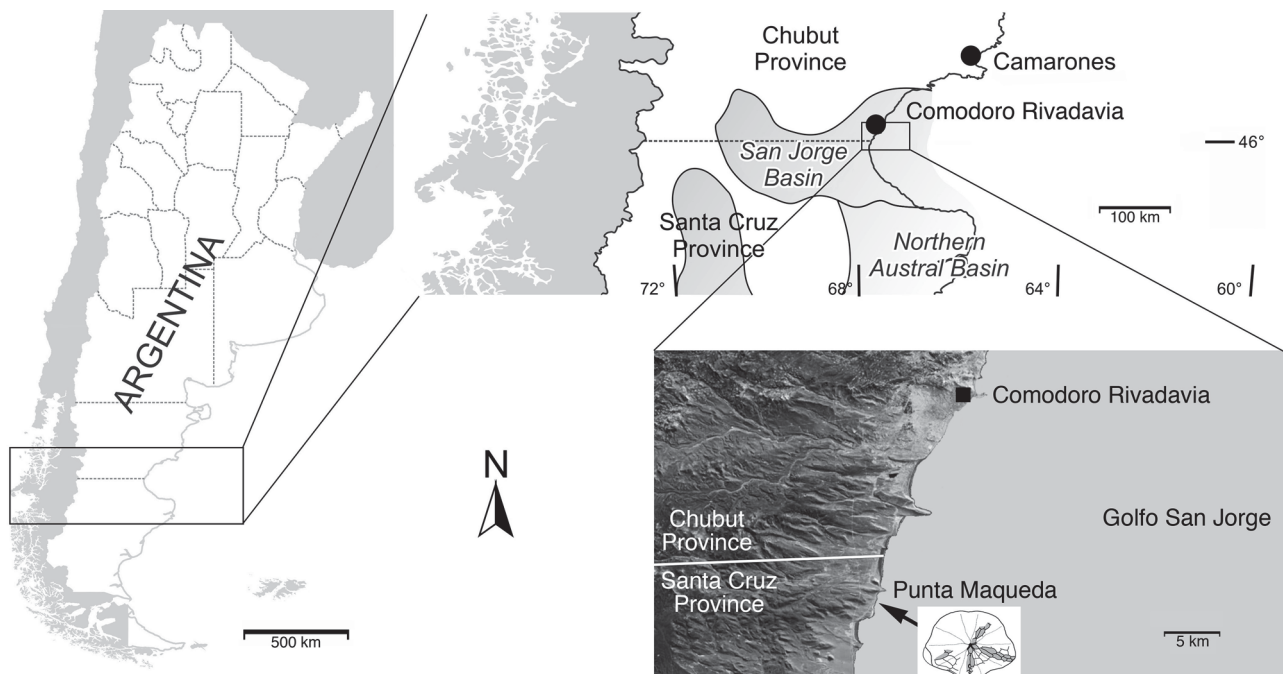


FIGURE 1. Locality (sand dollar with arrow) at which *Monophoraster telfordi* n. sp. has been collected. Location of the main Cenozoic basins modified from del Río (2004).

Geologic setting

The marine rocks that constitute the Chenque Formation in the San Jorge Basin (Chubut and Santa Cruz Provinces, Argentina) are well known through their palynological and molluscan content, but they also yield an interesting, highly diversified, locally abundant and almost unstudied echinoderm fauna represented by asteroids, ophiuroids and irregular echinoids. Echinoderms are common throughout the sequence in the basal beds of this unit, exposed about 2 km south of Punta Maqueda (Santa Cruz Province) (Fig. 1), and comprise a spectacular assemblage from which only *Ophiocrossota kollemborgorum* Caviglia *et al.*, 2007 has been described (Caviglia *et al.* 2007; Martínez *et al.* 2009). These fossiliferous strata correspond to the Parasequence I of the lowermost part of the Chenque (Bellosi 1990). This part is visible only during low tides, and consists of an intercalation 12 metres thick of grayish fine sandstones, with ocher and greenish, moderately fossiliferous sandstones deposited from distal lower shorefaces at the base, to a middle shoreface environment at the top of the section (Fig. 2). *Monophoraster* n.sp.

has been collected from one thin bed up to 15 cm thick and composed of very fine-grained sandstones (M4 in Fig. 2) containing ophiuroids, another as yet unidentified clypeasteroid echinoid, assemblages of oysters in life position, and clusters of *Atrina* sp.

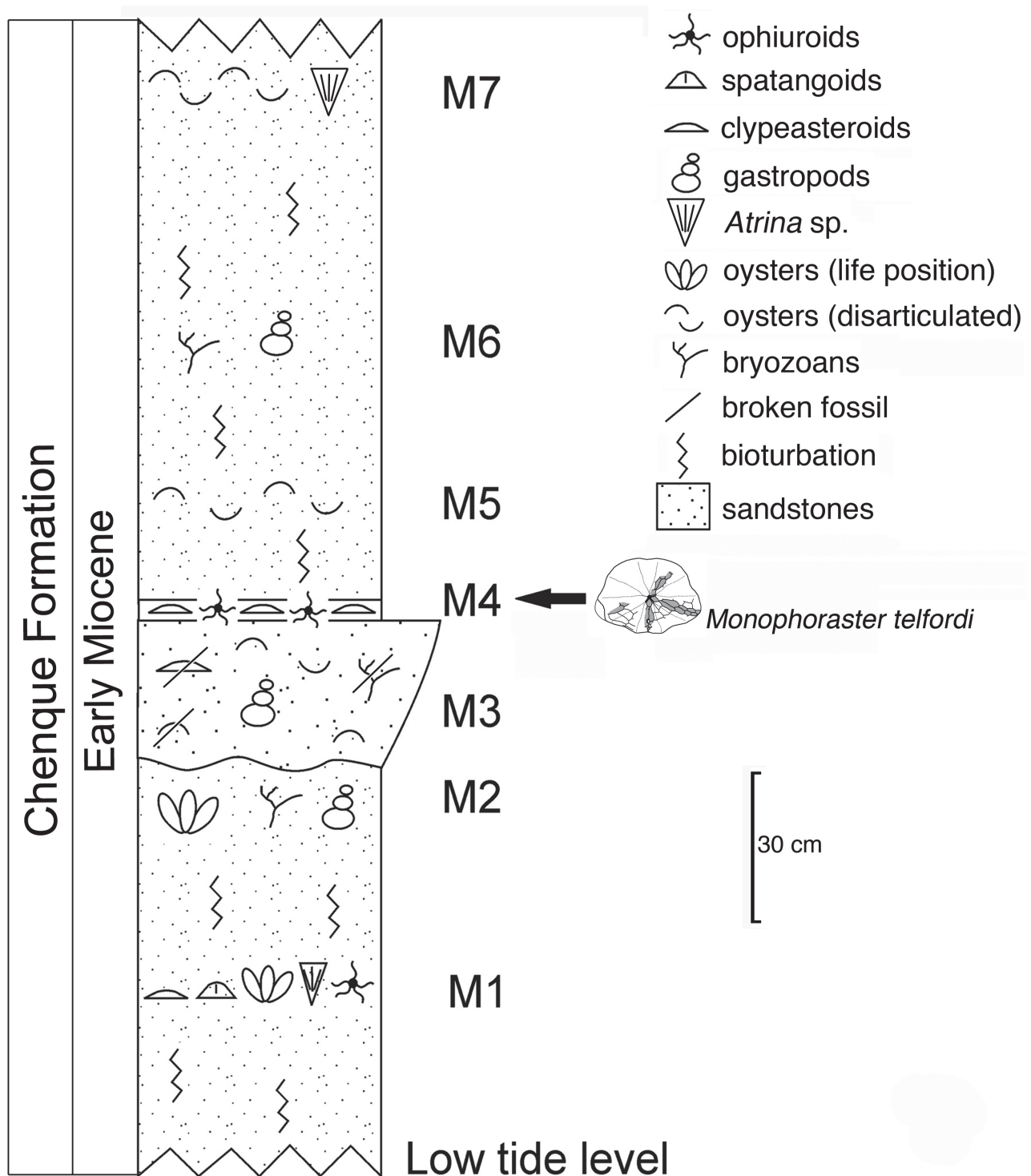


FIGURE 2. Stratigraphic section of the studied outcrop. M4 (sand dollar with arrow) indicates fossiliferous bed with *Monophoraster telfordi* n. sp. (after Martínez *et al.* 2009).

According to palynomorphs and the *Jorgechlamys juliana*-*Reticulochlamys borjasiensis* Molluscan Assemblage (del Río 2004) the horizons containing the new *Monophoraster* are Early Miocene, making this the oldest uncontested record of the genus in Patagonia. *Monophoraster darwini* has been also reported in the Middle Miocene sandstones that constitute the uppermost section of the Chenque Formation exposed to the north of Punta

Maqueda, at Estancia Busnadiago (Chubut Province), where it is associated with the bivalve *Venericor* as part of the *Nodipecten* sp.-*Venericor abasolensis*-*Glycymerita camaronesia* Assemblage (del Río, 2004). The youngest record for *Monophoraster* corresponds to the Late Miocene, when it became abundant as represented by *M. darwini* in the Puerto Madryn Formation (Chubut Province), and by *M. duboisi* in the Paraná Formation (Entre Ríos Province) and the Camacho Formation (Uruguay) (Mooi *et al.* 2000).

Systematic part

Class Echinoidea Leske, 1778

Irregularia Latreille, 1825

Order Clypeasteroida A. Agassiz, 1872

Suborder Scutellina Haeckel, 1896

Family Monophorasteridae Lahille, 1896

Genus *Monophoraster* Lambert and Thiéry, 1921

Diagnosis. Scutelline sand dollars with only a single lunule located in the posterior interambulacrum (interambulacrum 5), and a well-demarcated ridge around the lunule on aboral surface. Without pressure drainage channels leading to the anal lunule on the oral surface. First post-basicoronal plates in the interambulacra are elongated (a condition also found in *Iheringiella*). Interambulacra narrow considerably towards the ambitus, in some cases only a single plate spanning the entire interambulacrum.

Type species. *Monophoraster darwini* Desor, 1847, by monotypy of original description.

Monophoraster telfordi n. sp.

Figures 3, 4A–C

Diagnosis. *Monophoraster* with an alate test yielding a test width to length ratio of approximately 1.4:1, and with the paired interambulacra barely continuous with their corresponding basicoronal, in some cases with only one of the two post-basicoronals in contact with the basicoronal.

Etymology. Named after Dr. Malcolm Telford, retired professor of zoology at the University of Toronto, Canada, and a fellow echinologist who shed and shared with his students much light on sand dollar feeding as well as the evolution and function of lunules.

Types. Material is housed at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN). Holotype is MACN-Pi 5807, from shoreline deposits about 2 km south of Maqueda Point, Santa Cruz Province, southern Argentina. Chenque Formation, early Miocene. The paratype, MACN-Pi 5808, has the same provenance as the holotype.

Description. Test exceeding 65 mm in length (see Table 1 for measurements of holotype and paratype). Aboral surface slightly domed, oral surface flat (Fig. 3). Slight sinuosity to ambitus when viewed edge-on. Highest point of test located at apical system. Interambulacra 1 and 4 elongated relative to other interambulacra to produce wing-like, or alate morphology (*sensu* Mooi *et al.* 2000) when viewed from the aboral aspect. Test much wider than long, width to length ratio approximately 1.4:1. Broad but shallow marginal indentations present where perradial suture meets the ambitus in each ambulacrum. Small elongate or nearly circular anal lunule present in interambulacrum 5. Aboral perimeter of lunule pronounced to form strongly demarcated ridge (Figs. 3, 4A, B).

Apical system monobasal, slightly anterior, with numerous hydropores scattered over the madreporic plate (Fig. 3). Four gonopores, one in each of the paired interambulacra and located at the suture between the madreporic plate and the first adapical plates of the interambulacral column.

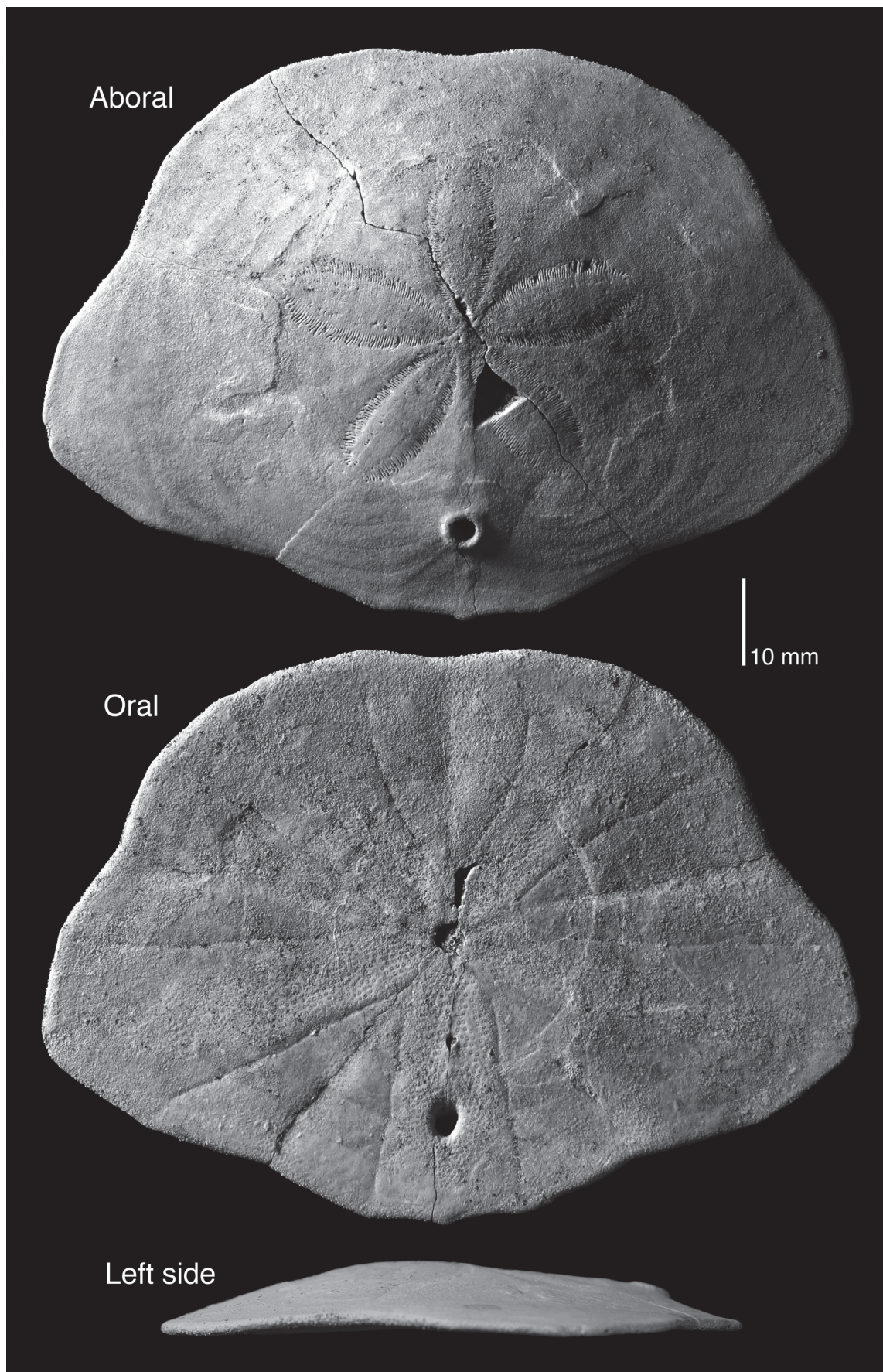


FIGURE 3. Photographs of the holotype MACN-Pi 5807 of *Monophoraster telfordi* n. sp.

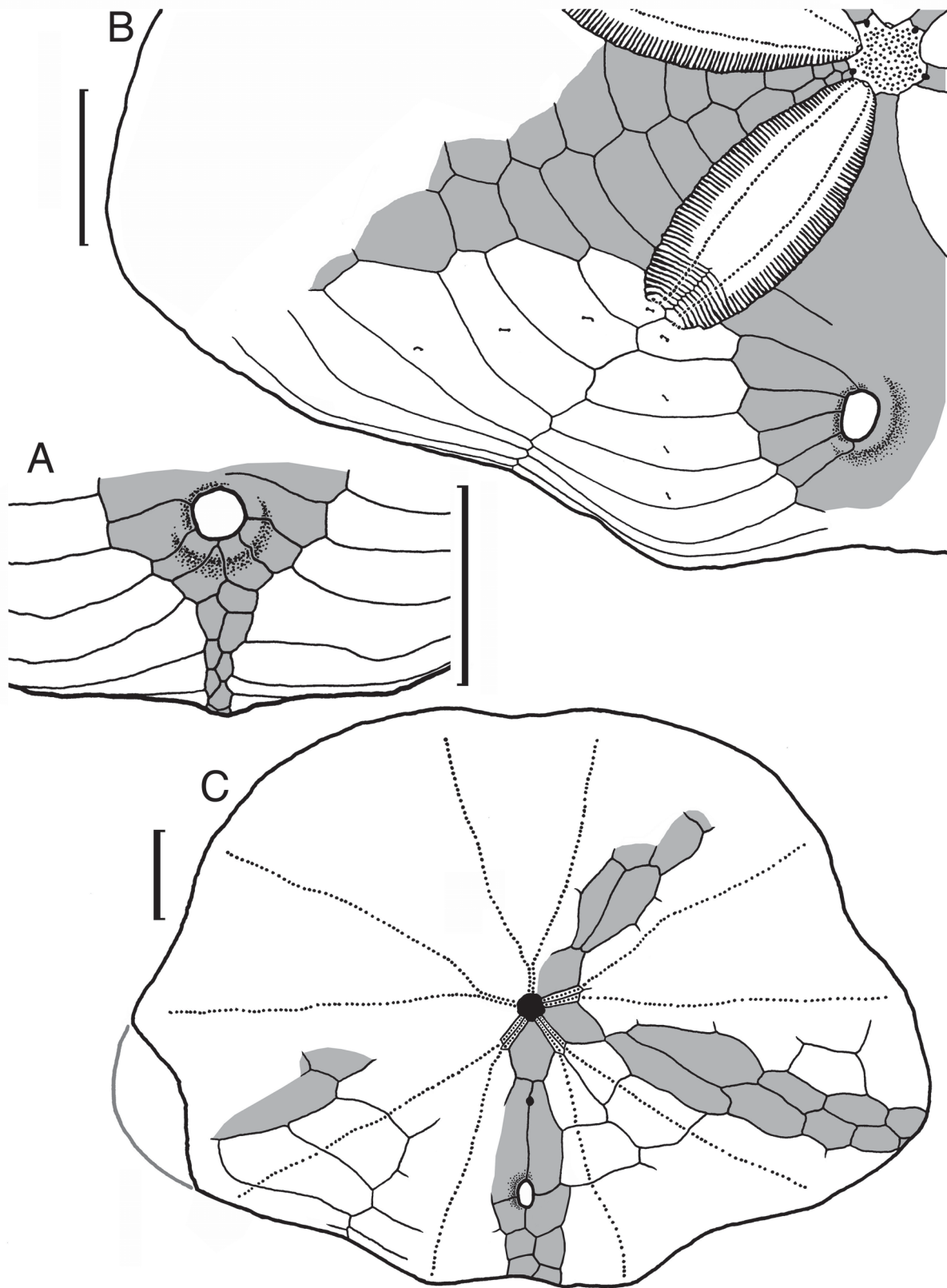


FIGURE 4. *Monophoraster telfordi* n. sp., details of discernible plate architecture (indistinct sutures omitted). A: Holotype MACN-Pi 5807, aboral plate architecture in the region around the anal lunule. B: Paratype MACN-Pi 5808, aboral plate architecture near the apical system and in ambulcra V and interambulacrum 4, as well as near the anal lunule region; C: Paratype MACN-Pi 5808, oral plate architecture and pathways of the main branches of the food grooves, test outline reconstructed in interambulacrum 1. Peristome and periproct in solid black, interambulacra shaded, all scale bars 10 mm in length.

Ambulacra petaloid adapically, extending about 47–55% of the corresponding test radius. Anterior unpaired petal (III) and posterior paired petals (I and IV) shortest, anterior paired petals longest. Petals lyrate, almost closed distally, with three or four trailing podia (*sensu* Mooi 1989) at the distal end of each column of respiratory podia (Fig. 4B). Respiratory podial pairs strongly conjugated, inner pore circular or almost circular, outer pore distinctly elongate, apparently subdivided by stereom septae. Five to eight occluded plates present at the tips of the petals (Fig. 4B). At the ambitus, ambulacra strongly widened, forming strip-like ambital plates (Fig. 4B). Ambulacra for which plate patterns could be discerned (Fig. 4C) all in agreement with Lovén's Rule (David *et al.* 1996). Ambulacral basicoronal plates all similar, narrow and straight with almost parallel radial sutures on each side (Fig. 4C). Interambulacral basicoronal plates almost equally developed, broad, and about twice as long as the ambulacral basicoronals (Fig. 4C).

Interambulacra narrow and straight, narrowing strongly towards the ambitus, but containing paired, zig-zag plates right up to the madreporic plate (Fig. 4B). On the oral surface, widest point is about midway along the first post-basicoronal plates and on the aboral surface, between the distal parts of the petals. Approximately four post-basicoronal plates in each half of interambulacral column on the oral surface. Paired interambulacra only about 10% the width of the ambulacra at the ambitus. Unpaired, posterior interambulacrum 5 greatly attenuated as it approaches the ambitus (Fig. 4C). On the aboral surface, narrowing of the interambulacra is most pronounced in interambulacrum 5, where it appears that in at least one case, only a single plate spans the interambulacrum circumferentially (Fig. 4A). Interambulacrum 5 broadly continuous with its corresponding basicoronal, paired interambulacra barely continuous, with only a narrow point of contact with the basicoronal, in at least one case (interambulacrum 4) in the paratype, only one of the two post-basicoronals contacts the basicoronal. Posterior interambulacrum of holotype pronounced into a shallow point (Fig. 3), but this is lacking in the paratype in which the posterior edge is markedly truncate (Fig. 4B, C).

Peristome circular, relatively small (Table 1), almost centrally situated on the oral surface, with a distinct perradial process in each ambulacrum extending into the peristome beyond the slight bulge containing the sphaeridium. Periproct small (Table 1), close to the edge of the basicoronal in interambulacrum 5, placed about halfway (or slightly more anteriorly) between the anterior edge of the anal lunule and the peristome but not associated with a channel leading to the lunule. Slight ridge or faring at posterior edge of periproct (Fig. 3). Periproct wholly contained between first post-basicoronals in interambulacrum 5 along interradian suture.

Aboral tuberculation homogeneous. Clearly differentiated geniculate, pressure drainage channel, and locomotory spine fields on oral surface (Fig. 3). No discernible spination remains on the specimens. In several places on the oral surface, distinct tube foot pores are visible in the food grooves, and in the geniculate spine regions that are strongly developed on either side of the branches of the food grooves.

Food grooves well developed (Figs. 3, 4C), restricted to the oral surface, with primary bifurcation near the distal ends of the ambulacral basicoronal plates. After this branch point, food grooves continuously diverge as they approach the ambitus to form pronounced V-shapes in paired ambulacra, but each branch converges slightly in the anterior, unpaired ambulacrum III of the holotype (Fig. 3). Secondary branching is faint, likely due to diagenetic processes that pressed surrounding sand grains into many parts of the test surface. Pressure drainage channels (*sensu* Telford 1988) strongly developed along perradial sutures on oral surface from ambitus adorally to a gore point just short of the bifurcation of the main branches of the food grooves. No pressure drainage channel associated with the anal lunule.

Occurrence. Known only from the type locality.

Discussion. *M. telfordi* differs from both *M. darwini* and *M. duboisi* in its relatively widened test and more weakly expressed continuity of the paired interambulacra on the oral surface. Members of the genus *Monophoraster* are easily distinguished from those in *Amplaster* in part by the dramatic widening of the test in the latter. As noted, the new species, *M. telfordi*, also has a very wide test, which slightly blurs the distinction between the two taxa. However, as in *Monophoraster darwini*, the periproct of *M. telfordi* is much further from the lunule than in any species of *Amplaster*, strongly suggesting that the new species should be placed in *Monophoraster*.

Among *Amplaster*, *A. alatus* is most similar to *M. telfordi* in overall shape and in width to length ratio. However, in *M. telfordi* this ratio still falls well short of that in *A. alatus*. In addition, there is very distinct and broad continuity between the first post-basicoronals and the basicoronals in all interambulacra among *Amplaster* species. In fact, among monophorasterids, only *M. telfordi* is known to express narrow connections between post-basicoronals and the basicoronals, or in having only one of the two post-basicoronals in contact with the basicoronal.

TABLE 1. *Monophoraster telfordi* n. sp.: measurements (in mm, except for ratio) of the holotype and paratype.

	Holotype (MACN-Pi 5807)	Paratype (MACN-Pi 5808)
Test Length	65.4	66.7
Test Width (estimated for paratype by doubling width of left side of test to center of peristome)	94.8	96.0
Test Height (at apical system)	7.3	6.5
Ratio of Test Width to Length	1.44	1.43
Apex Position (from anterior edge of test to anterior edge of madreporic plate)	31.7	33.5
Anal Lunule Length	2.4	3.3
Anal Lunule Width	2.6	2.5
Anal Lunule Position (from anterior edge of test to anterior edge of lunule)	53.6	55.1
Ambulacrum I Length (from corresponding ocular to intersection of perradial suture and ambitus)	32.2	31.9
Ambulacrum II Length (from corresponding ocular to intersection of perradial suture and ambitus)	38.5	39.7
Ambulacrum III Length (from corresponding ocular to intersection of perradial suture and ambitus)	31.7	33.3
Petaloid I Length	17.6	18.1
Petaloid I Width (at widest point)	8.5	7.6
Petaloid I Interporiferous Zone Width (at widest point)	3.8	3.2
Petaloid II Length	18.4	21.2
Petaloid II Width (at widest point)	9.0	8.5
Petaloid II Interporiferous Zone Width (at widest point)	3.9	4.1
Petaloid III Length	17.3	19.8
Petaloid III Width (at widest point)	8.3	8.3
Petaloid III Interporiferous Zone Width (at widest point)	4.1	4.5
Peristome Length	3.0	3.0
Peristome Position (anterior edge of test to anterior edge of peristome)	30.6	33.2
Periproct Length	1.2	1.1
Periproct Position (anterior edge of test to anterior edge of periproct)	43.5	45.3

Phylogenetically, synapomorphies for *Monophoraster* are expressed in the extreme narrowing of the interambulacra as they approach the ambitus, and in the degree to which the ambulacra are indented at the ambitus (Mooi *et al.* 2000). Although present, these characters are not strongly expressed in *M. telfordi*, and there is also some question that all specimens of *M. darwini* illustrate these features as distinctly as the specimens discussed in Mooi *et al.* (2000). Solely on the basis of the characters discussed in Mooi *et al.* (2000), it is not possible to say for certain whether *M. telfordi* falls to the base of the *Monophoraster* clade, or whether it could have an exclusive sister group relationship to either *M. darwini* or *M. duboisi*. Therefore, the trichotomy among *M. darwini*, *M. duboisi*, and *M. telfordi* remains unresolved at this time. Interestingly, the fact that *M. telfordi* is the oldest member of the genus is consistent with a hypothesis that some degree of widening of the test is plesiomorphic for the family.

Within the Clypeasteroidea, extreme test widening is known only among members of the Scutellina (*sensu* Mooi 1989). Mooi *et al.* (2000: 278) suggested that an increase in the relative width of the test in *Amplaster* “enhanced the rate at which new particles were encountered per unit surface area of the podial field”. *M. telfordi* is not only widened, it is like all monophorasterids and mellitids in possessing strongly developed fields of food-gathering tube feet that are concentrated in regions populated by geniculate spines on the oral surface. Specialized podial fields are also found primarily among the scutellines (although highly specialized but very differently organized, non-homologous food-gathering systems are seen among arachnoidids). Such fields are responsible for

collecting food particles according to the podial particle picking model described by Telford *et al.* (1985). Alate morphology in which the test is strongly widened is now also known among unrelated North and South American species of *Abertella* and *Eoscutella* (Durham 1955; Parma 1985; Osborn & Ciampaglio 2010), suggesting that adaptations increasing the rate at which podial particle picking fields can encounter new food particles arose several times independently among scutellines.

Key to species of Monophorasteridae

1. Test width to length ratio 1.5 or greater; periproct less than its own diameter distant from or on slope towards anterior edge of anal lunule 2
- 1'. Test width to length ratio less than 1.5; periproct at least its own diameter distant from anterior edge of anal lunule 4
2. Test width to length ratio 3.0 or greater *Amplaster coloniensis*
- 2'. Test width to length ratio between 1.5 and 2.5 3
3. Test width to length ratio between 1.5 and 2.0 *Amplaster alatus*
- 3'. Test width to length ratio between 2.0 and 2.5 *Amplaster ellipticus*
4. Test width to length ratio greater than 1.3; paired interambulacra barely continuous with basicoronal plate, each first post-basicoronal forming narrow contact point with basicoronal, or one of two post-basicoronals not in contact
..... *Monophoraster telfordi* n. sp.
- 4'. Test width to length ratio less than 1.3; both first post-basicoronal plates in each interambulacrum broadly in contact with the basicoronal 5
5. Peristome length greater than half the length of ambulacral basicoronals; test highly arched and smoothly convex over its entire length. *Monophoraster duboisi*
- 5'. Peristome length much less than half the length of ambulacral basicoronals; test low with slight flattening towards the ambitus, particularly posteriorly *Monophoraster darwini*

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